DIFFERENTIAL TIMING OF SPRING MIGRATION IN WOOD WARBLERS (PARULINAE)

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ABSTRACT.—Spring migration patterns of 18 species of paruline warbler at Prince Edward Point, Ontario showed that males arrived earlier than females in all species. Adult males arrived significantly earlier than second-year males in American Redstarts (*Setophaga ruticilla*), and there was evidence for a similar trend in other species. The difference in mean arrival dates between the sexes was greatest in species that arrived earliest. Similarly, within species, the difference between sexes was greatest in years when the males arrived earliest. For individuals within a species there was a significant negative correlation between arrival date and wing length; however, males of a particular size generally arrived earlier than females of the same size. Thus, larger size may be an advantage to early arrival, but is not sufficient to explain the difference in arrival between sexes. Species that winter furthest north arrived earliest, but sexual differences in wintering grounds have not been reported. These results are consistent with the hypothesis that males are selected to arrive as early as food resources or climatic conditions are adequate, whereas females arrive later, closer to the time when they can successfully begin nesting. *Received 19 August 1985, accepted 11 February 1986.*

IN most bird species males migrate earlier than females in spring (e.g. Chapman 1894, Gätke 1895, Jones 1895). Recent studies, however, have shown that this pattern was not true for all species. Early male arrival has been documented for many passerines (examples in Gauthreaux 1982) and several nonpasserines, including American Kestrels (*Falco sparverius*; Mills 1976), Common Shelducks (*Tadorna tadorna*; Patterson 1977), and various shorebirds (Greenhalgh 1968; Myers 1981a, b). The situation is reversed in some species, with females arriving before males in some phalaropes (Reynolds et al. 1986), Spotted Sandpipers (*Actitis macularia*; Oring and Lank 1982), Common Nighthawks (*Chordeiles minor*; Rust 1947), and possibly some raptors [immature Eurasian Sparrowhawks (*Accipiter nisus*); Moritz and Vauk 1976]. In species that mate for life or pair before arrival on the breeding grounds, the sexes apparently migrate at the same time [e.g. Snow Geese (*Chen caerulescens*), Cooke et al. 1975; Brewer's Blackbirds (*Euphagus cyanocephalus*), Orians 1980].

Several hypotheses can be formulated to explain differential timing of migration. One sex may migrate early because (1) it experiences greater intrasexual competition for territories or mates on the breeding grounds (e.g. Lincoln 1950); (2) it is larger and can tolerate harsher conditions early in the season (Ketterson and Nolan 1976, 1983); or (3) it is the dominant sex, allowing it to winter further north and thus reach the breeding grounds earlier (Ketterson and Nolan 1976; Gauthreaux 1978, 1982). Interactions between these factors are also possible, as selection for early arrival could influence size dimorphism or the choice of wintering grounds.

Myers (1981a) tested hypotheses similar to these with respect to sexual differences in the wintering range and arrival dates of shorebirds. He found that the territorial sex wintered further north and arrived earlier, irrespective of the relative sizes of the sexes and their apparent dominance relationships. This is most consistent with the first hypothesis. Arrival times for Spotted Sandpipers (Oring and Lank 1982), a species in which the female is territorial, also support this hypothesis. Recent data on phalaropes, which are not territorial, suggest that intrasexual competition for mates (as opposed to territories) can result in early arrival of one sex (in this case females; Reynolds et al. 1986).

Although many life-history studies of individual passerine species have noted that males arrive first on the breeding grounds (e.g. Bent 1953, Gauthreaux 1982), few have been quantitative, and none compared patterns across a broad range of species. We examined patterns of spring migration in North American wood warblers (subfamily Parulinae), passing through

southern Ontario. In all species considered, males are larger than females, on average, and are strongly territorial (Bent 1953).

Methods

The study was carried out at Prince Edward Point Bird Observatory, near Kingston, Ontario (43°57'N, 76°54'W). Warblers were caught primarily in 30-mm mesh mist nets, but some were also caught in a Heligoland trap. The habitat and netting areas are described in detail by Weir et al. (1980).

Each bird was banded with a U.S. Fish and Wildlife Service numbered band, and its unflattened wing chord was measured to the nearest millimeter. Sex was determined by criteria in the standard banding manuals (Wood 1969, Sheppard and Klimkiewicz 1976, Can. Wildl. Serv. and U.S. Fish & Wildl. Serv. 1977): most species were sexed by plumage characters, although Tennessee Warblers (see Table 1 for scientific names) were sexed by wing chord (≤60 mm for females; ≥64 mm for males). Age was determined only in male American Redstarts, in which males in their second calendar year (SY) have a femalelike plumage that is quite distinct from the black and orange of the after-second-year (ASY) males (Ficken and Ficken 1967).

Netting was carried out during spring migration in 1976–1980. Nets were set irregularly in April (mainly on weekends) and daily from 1 May (6 May in 1979) until at least 10 June, by which time the majority of the late species had arrived (e.g. see Fig. 1f). Fifteen to 30 12-m nets were set daily, except in 1976 when a maximum of 10 nets was in use at any one time.

Because we were interested primarily in the relative arrival dates of the sexes, and the netting effort was distributed fairly uniformly throughout most of the season, the raw banding totals were used for analysis. We did not standardize by calculating birds per net hour because this index may vary considerably depending on net location, time of day, and weather conditions in addition to the number of birds actually present. Without detailed information on the timing and use of nets and how many birds were caught in each net, a simple index could introduce more biases than it corrects.

To further minimize the effect of fluctuations in trapping effort and to increase sample sizes for less common species, data were pooled for all five years. Because mean arrival dates varied among years, probably due partly to weather conditions (see Richardson 1978), pooling tended to increase the variance in arrival dates. However, the individual dates were not standardized to the mean arrival date for the year for two reasons. First, the mean arrival for the sample in a particular year was affected by differences in trapping effort as well as differences in the population

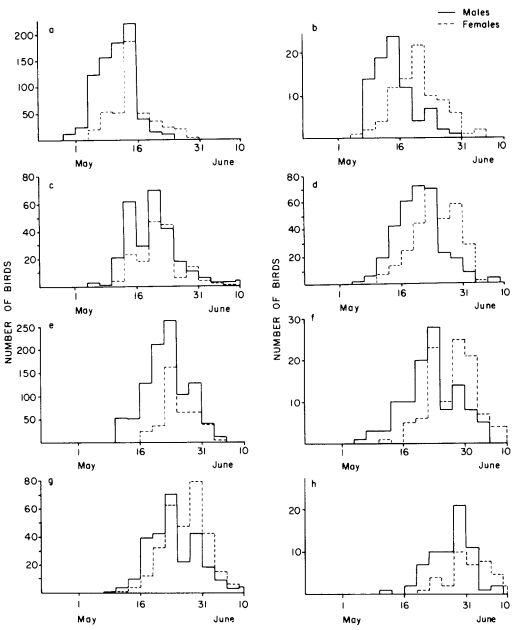

Fig. 1. Numbers of each sex for representative species of warblers captured at Prince Edward Point, 1976–1980 (3-day totals). (a) Yellow-rumped Warbler, (b) Black-and-white Warbler, (c) Yellow Warbler, (d) Common Yellowthroat, (e) Magnolia Warbler, (f) Blackburnian Warbler, (g) American Redstart, (h) Mourning Warbler.

arrival. Second, the relative means for the sexes could be affected differently in each year.

To examine whether the location of breeding or winter ranges influenced variation in arrival dates among species, we estimated both of these ranges from the literature. The approximate northern and southern breeding latitudes in Ontario and Quebec were estimated from range maps in Peterson (1980). For species that breed south of the study area, the latitude of Prince Edward Point was taken as the southern limit (44°N). The northern and southern limits of the normal wintering range were estimated from the A.O.U. Check-list (A.O.U. 1983).

Results

Overall pattern.—A total of 7,966 warblers of 34 species was caught and banded in the springs of 1976–1980. Of these, 16 species were excluded from analysis because they could not be sexed reliably based on external characters or because they were caught in small numbers (less than 10 of each sex). Few warblers were recaptured after initial banding, indicating that most birds did not remain more than one or two days

TABLE 1. Spring migration dates of male and female paruline warblers at Prince Edward Point, Ontario, 1976–1980.[a]

Species	Males		Females		P[b]
1. Yellow-rumped Warbler (*Dendroica coronata*)	9.4 ± 4.6	(784)	13.4 ± 5.0	(439)	**
2. Black-and-white Warbler (*Mniotilta varia*)	13.1 ± 4.9	(83)	19.0 ± 6.0	(83)	**
3. Nashville Warbler (*Vermivora ruficapilla*)	13.6 ± 5.4	(216)	19.0 ± 5.0	(104)	**
4. Cape May Warbler (*Dendroica tigrina*)	16.1 ± 5.5	(58)	21.6 ± 3.8	(55)	**
5. Black-throated Blue Warbler (*Dendroica caerulescens*)	17.2 ± 6.6	(63)	22.9 ± 5.3	(109)	**
6. Yellow Warbler (*Dendroica petechia*)	18.5 ± 6.1	(271)	20.2 ± 5.0	(164)	**
7. Common Yellowthroat (*Geothlypis trichas*)	18.8 ± 5.6	(321)	23.0 ± 5.3	(293)	**
8. Black-throated Green Warbler (*Dendroica virens*)	20.0 ± 6.7	(193)	24.0 ± 6.4	(98)	**
9. Chestnut-sided Warbler (*Dendroica pensylvanica*)	20.3 ± 6.1	(115)	25.4 ± 5.6	(44)	**
10. Tennessee Warbler (*Vermivora peregrina*)	21.0 ± 3.3	(50)	23.2 ± 3.9	(48)	**
11. Magnolia Warbler (*Dendroica magnolia*)	21.2 ± 5.4	(995)	24.1 ± 3.9	(396)	**
12. Blackburnian Warbler (*Dendroica fusca*)	21.6 ± 6.5	(110)	27.0 ± 5.7	(106)	**
13. American Redstart (*Setophaga ruticilla*)	22.7 ± 5.8	(262)	25.7 ± 5.2	(304)	**
14. Wilson's Warbler (*Wilsonia pusilla*)	23.0 ± 5.1	(209)	25.1 ± 4.2	(30)	*
15. Bay-breasted Warbler (*Dendroica castanea*)	23.3 ± 4.0	(186)	24.7 ± 3.5	(132)	*
16. Canada Warbler (*Wilsonia canadensis*)	24.4 ± 4.7	(217)	27.6 ± 4.4	(125)	**
17. Mourning Warbler (*Oporornis philadelphia*)	26.1 ± 5.0	(65)	30.4 ± 5.3	(38)	**
18. Blackpoll Warbler (*Dendroica striata*)	26.9 ± 3.5	(26)	28.8 ± 4.3	(19)	NS

[a] Mean date in May ± SD (sample size).

[b] Probability that the distribution of arrival dates differs between the sexes (median test): * = $P < 0.05$, ** = $P \ll 0.01$, NS = not significant.

at Prince Edward Point. Thus, we used banding date as the date of arrival.

In all species examined, the mean arrival date for males preceded that for females (Fig. 1, Table 1). This difference was statistically significant in all species except the Blackpoll Warbler, which had the smallest sample size. The magnitude of the difference between sexes ranged from 1.7 to 5.9 days.

Generally, the mean arrival date of the sexes differed most in species that arrived early and less in late-arriving species (Fig. 2; correlation between mean male arrival date and sexual difference: $r = -0.54$, $P = 0.03$, $n = 18$). Furthermore, two of the species that deviated most from this trend, the Yellow-rumped and Yellow warblers, were potentially affected by biases in the sampling. Yellow-rumped Warblers were the earliest migrants, and many arrived in April before the start of intensive netting. Thus, the mean arrival date of males was probably earlier than recorded, and this would have resulted in a greater difference between the sexes. Yellow Warblers, on the other hand, are the only species that breeds commonly around the netting area (Sprague and Weir 1984). Therefore, many birds may have been caught well after their initial arrival when both sexes were already present, thus reducing the difference in capture dates between the sexes. If these two species are excluded, the correlation between male arrival date and the difference in arrival between the sexes is much stronger ($r = -0.71$, $P < 0.002$, $n = 16$).

Annual variation within species.—To examine year-to-year variation, we measured deviations in the mean arrival dates in each year from the overall 5-yr means for each species. Because the dates were thus standardized among species, and because 5 yr provides insufficient degrees of freedom to examine each species separately, we considered all of the species together to look for overall trends. Excluding values when fewer than 5 birds of either sex were caught in a given year, the difference between the sexes was negatively correlated with the relative date of arrival of the males ($r = -0.51$, $P < 0.001$, df = 57). Thus, within species, the difference in mean arrival dates between the sexes was greatest in years when the males arrived earliest.

Range of migration dates.—To control for differences between years in mean arrival dates of males and females, we compared the sexes in each year. Including all species, the standard deviation for males was greater in 48 of 77 cases when 5 or more of each sex were caught. This differs significantly from equality (binomial test, $\chi^2 = 4.6$, $P < 0.05$). The midquartile range was greater for males in only 38 cases, how-

ever, and equal in another 6. This does not differ significantly from equality ($\chi^2 = 0.35$, $P > 0.50$).

The difference between these two tests can be explained by the non-normal distribution of the arrival dates (Fig. 1). The midquartile range is unaffected by extreme values, whereas the standard deviation can be markedly increased by outliers. This suggests that, overall, most males and females arrive in a similar time span; early or late males, however, arrive over a greater range of dates than do females.

Effect of size.—Wing length, which is strongly correlated with lean body weight within species (Connell et al. 1960, Rogers and Odum 1964), was used as an index of body size. At Prince Edward Point, the wing length of an individual within each sex was significantly correlated with its date of capture for most species (Table 2). The correlations were often quite weak, but in all cases they were negative, indicating that larger birds tended to arrive earlier than smaller ones. The correlation coefficients were generally higher for males than for females.

Because large birds tended to arrive earlier, and males are larger than females (see Table 2), size differences alone might account for the earlier arrival of males. To test this, we compared the arrival dates of males and females using analysis of covariance (ANCOVA) to correct for size differences. The results varied somewhat among species (Table 2). In a few cases the size hypothesis was supported (e.g. Black-throated Green and Bay-breasted warblers), but for most species arrival dates for each sex were still significantly different after allowing for size variation. For three species, the slopes of the regressions relating wing length to arrival date differed between the sexes, invalidating the assumptions of analysis of covariance. In these three cases, however, arrival dates of females varied little with wing length, also indicating that wing length is insufficient to explain the difference between sexes.

Because larger birds within a species tended to arrive earlier, size differences among species might account for differences in their mean arrival dates. When all 18 species were compared, however, there was no significant correlation between mean wing length of males of a species and their mean arrival date ($r = -0.09$, $P > 0.70$). Species with the greatest sexual size dimorphism also might be expected to have the greatest difference between males and females in arrival dates, but there was no significant correlation between the size dimorphism of the sexes (ratio of female to male wing length) and the difference in mean arrival times between sexes ($r = 0.29$, $P > 0.25$).

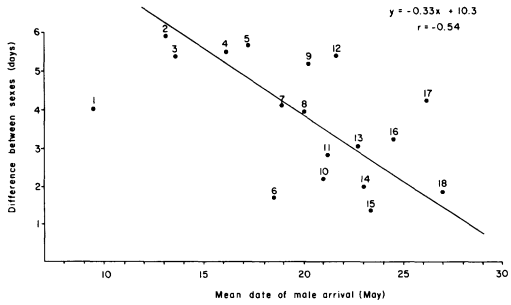

Fig. 2. Differences in mean arrival dates of the sexes relative to mean arrival date of males. The regression line is the geometric mean regression because both values are random variables. Numbers correspond to species in Table 1.

Age effects.—Second-year males were distinguished from ASY males only in the American Redstart. For this species the arrival dates for the ages differed significantly (Fig. 3; median test, $\chi^2 = 35.0$, $P < 0.0001$). The mean date of arrival of SY males (25.1 May, $n = 118$) was about 4 days later than ASY males (20.7 May, $n = 144$). The later peak arrival for SY males (Fig. 3) is apparent as a second, lower peak in the overall totals for male redstarts (Fig. 1g).

The mean wing length of SY male redstarts (60.7 mm, $n = 117$) was significantly shorter than that of adults (61.7 mm, $n = 144$; $t = 3.3$, $P < 0.001$). The smaller size and later arrival of SY males explains part of the correlation between size and date of arrival but, although there was no significant correlation between arrival date and wing length for SY males, there was a significant correlation for ASY males ($r = -0.23$, $P < 0.01$). Analysis of covariance, standardizing for wing length, showed that size differences alone were insufficient to explain the difference in mean arrival times between age groups ($F = 5.9$, $P = 0.01$).

There is also indirect evidence that SY males arrived later than ASY males in other warblers. Eight species showed a distinct second peak of male arrivals (e.g. Fig. 1b, e, f) similar to that of SY American Redstarts (Figs. 1g and 3). Fur-

TABLE 2. Mean wing lengths of male and female warblers, and the correlation (r) between wing length and date of capture at Prince Edward Point.

Species	Wing length (mm)		r[a]		ANCOVA[b]	
	Males (n)	Females (n)	Males	Females	F	P
Yellow-rumped Warbler	72.0 (784)	68.6 (438)	−0.19**	−0.12**	72.2	**
Black-and-white Warbler	68.0 (83)	65.6 (83)	−0.30**	−0.41**	15.5	**
Nashville Warbler	58.5 (215)	55.8 (102)	−0.21**	NS	36.5	**
Cape May Warbler	65.8 (58)	63.5 (55)	−0.27*	NS	20.3	**
Black-throated Blue Warbler	63.7 (63)	60.8 (107)	NS	NS	14.3	**
Yellow Warbler	61.5 (269)	58.7 (161)	−0.32**	−0.24**	1.1	NS
Common Yellowthroat	55.0 (315)	52.0 (291)	−0.17**	−0.21**	—	
Black-throated Green Warbler	61.3 (192)	58.8 (95)	−0.34**	NS	2.5	NS
Chestnut-sided Warbler	62.2 (114)	59.5 (43)	−0.44**	NS	—	
Magnolia Warbler	58.9 (992)	56.5 (391)	−0.29**	−0.14**	—	
Blackburnian Warbler	67.4 (109)	63.5 (106)	−0.43**	NS	4.2	*
American Redstart	61.3 (259)	58.8 (302)	−0.21**	−0.16**	13.4	**
Wilson's Warbler	53.9 (209)	51.3 (30)	−0.27**	NS	0.3	NS
Bay-breasted Warbler	73.2 (186)	69.6 (131)	−0.43**	−0.21*	0.1	NS
Canada Warbler	63.9 (216)	61.2 (124)	−0.22**	NS	8.5	*
Mourning Warbler	60.8 (65)	57.9 (38)	−0.50**	NS	—	
Blackpoll Warbler	72.9 (26)	68.5 (19)	NS	−0.55*	0.1	NS

[a] * = $P < 0.05$, ** = $P \ll 0.01$, NS = not significant.

[b] Probability that sexes differ in arrival date after adjusting for differences in wing length (— indicates ANCOVA invalid because the slopes were not parallel).

thermore, if the young in those species also have shorter wing lengths than adults (as is true for many other birds; Nisbet et al. 1963, Stewart 1963, Pienkowski and Minton 1973), then the late arrival of SY males could partly explain the negative correlation between wing length and arrival date within each sex.

Breeding and wintering distribution.—The estimated northern limit of the breeding range for each of the 18 species was between 50°N and 58°N, while the southern limit ranged from 44°N to 50°N. Neither limit was significantly correlated with the mean date of arrival of the males (north: $r = 0.04$, $P > 0.80$; south: $r = 0.36$, $P > 0.10$). This result must be interpreted cautiously, however, because the actual destinations of the birds caught at Prince Edward Point were not known and could have been quite different from the species limits as a whole.

The limits of the wintering distribution were more variable, ranging from about 40°N to 10°N for the northern limit and from 14°N to 25°S for the south. The northern limit for each species was strongly and negatively correlated with the mean date of male arrival ($r = -0.75$, $P < 0.001$); however, the correlation with the southern limit was not quite significant ($r = -0.46$, $P = 0.054$). Thus, the species that winter furthest north arrive earliest in spring at Prince Edward Point (Fig. 4).

DISCUSSION

On average, male warblers arrive before females at Prince Edward Point, in agreement with previous accounts for individual warbler species (e.g. Bent 1953, Nolan 1978). There was significant variation within and among species in the magnitude of the differences between the sexes. The patterns of variation can be used to test predictions from various hypotheses about the evolution of differential migration. We shall base our discussion of these hypotheses on the relative costs and benefits for each sex of early arrival on the breeding grounds (assuming that passage migration times reflect arrival times on the breeding grounds). We shall consider first some of the potential costs and benefits, then how various factors might cause them to differ between the sexes. Although we cannot conclusively support or reject these hypotheses, we present this discussion to stimulate interest in a topic that has received relatively little recent attention.

Costs and benefits of early arrival.—The costs of early arrival have not been measured directly, but Nolan (1978) and Lank et al. (1985) considered food availability on the breeding grounds. Both studies showed that the first birds arrive when food is very scarce, whereas later in the season, when nesting starts, food is relatively

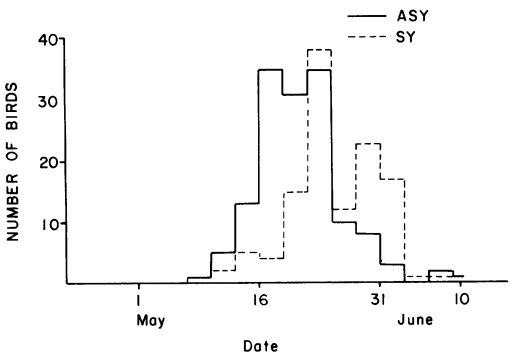

Fig. 3. Numbers of second-year (SY) and after-second-year (ASY) male American Redstarts captured at Prince Edward Point, 1976–1980 (3-day totals).

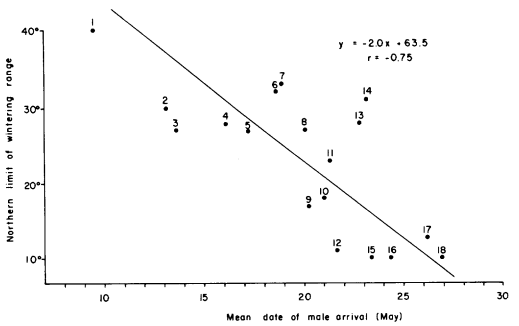

Fig. 4. Relationship between mean date of male arrival at Prince Edward Point and the northern limit of the breeding range. Numbers correspond to species in Table 1.

abundant. In addition, early in spring there is an increased risk of severe storms or cold weather that can cause significant mortality in small passerines (e.g. see Whitmore et al. 1977). Thus, the potential costs of early arrival include poor nutrition or even starvation, as well as risks associated with colder weather and late storms.

The fact that some birds arrive before conditions are suitable for nesting suggests that the benefits are sufficient to balance these costs. The most obvious benefits are due to intrasexual competition. Birds that arrive early may have more opportunities to acquire high-quality territories or mates.

Size differences.—Differential migration could arise if the benefits of early arrival are equal for all birds, but the costs are lower for one sex. Because male warblers are larger, they may be better able to tolerate harsh weather (Ketterson and King 1977) and thus reduce the risks of early arrival. We found, however, that the differences in arrival dates between the sexes were greater than could be accounted for by size alone (as measured by wing length; Table 2). Furthermore, there was no relationship across species between the degree of dimorphism and the magnitude of the difference in arrival times between the sexes. Thus, size dimorphism alone does not fully explain differential migration.

Nevertheless, the tendency for larger individuals within each sex to arrive earlier suggests that size may be important. Part of the observed relationship between wing length and arrival date may be due to the shorter wings and later arrival of SY birds, but in ASY male American Redstarts there was still a significant correlation between size and arrival times. If wing lengths continue to increase after the first year [as in Red Knots (*Calidris canutus*); Pienkowski and Minton 1973], there could be a continuing age effect. Alternatively, if some individuals are more tolerant of cold, their costs for early arrival could be lower, leading to individual variation in the optimal arrival date.

Winter distribution.—Differences in the distance each sex has to travel also could result in differential timing of arrival. The correlation between wintering latitude of a species and its mean arrival date (Fig. 4) suggests that differences in wintering latitude between the sexes could influence their arrival dates. If this led to arrival at a time that otherwise would be suboptimal, then selection might influence the departure time from the wintering grounds, unless there were other constraints during migration. In at least one Asian warbler, *Acrocephalus orientalis*, males depart on spring migration before females from areas where they winter together (Nisbet and Medway 1972). Furthermore, there is little evidence that male and female paruline warblers differ in their wintering ranges, so this hypothesis seems unlikely to fully explain the differences in their arrival dates.

Intrasexual competition.—Differential migration also could arise if one sex benefited more from early arrival than the other. Male warblers compete for territories, and the first bird to arrive on a territory usually has an advantage in defending it (e.g. see Orians 1980). Female intrasexual competition has not been well

documented but probably occurs. Various factors such as male-biased sex ratios or polygyny, however, could lower the intensity of female competition. Stewart and Aldrich (1951) found many surplus males in a spruce-fir warbler community, while Ficken and Ficken (1967) and Proctor-Gray and Holmes (1981) found unpaired territorial male American Redstarts, suggesting a shortage of females. Nolan (1978) reported polygyny in Prairie Warblers (*Dendroica discolor*), and it probably occurs in other species. Obviously, there could still be some competition among females for the best males, but the cost of "losing" would be reduced. A late-arriving female might suffer the cost of breeding with an inferior or polygynous male, but a late male might not have an opportunity to breed at all.

If the benefits of early arrival are less significant for females, factors such as food availability and the risk of poor weather become more important. Thus, females would arrive later, closer to the time when sufficient food reserves are available for nesting and egg production. In this case, the magnitude of the difference in arrival dates between the sexes would be related to the rate of change of food availability and climate. The greater differential between the sexes in early migrants is consistent with the greater risk of severe storms early in the season. More data on seasonal increases in insect abundance are required, however, to test the prediction for food.

Even if females compete intensely with each other for mates, they might not benefit by arriving before the males have established territories. This would also lead to differential migration, but in this case the magnitude of the difference in arrival times between the sexes would be proportional to the length of time required for territory establishment. Further data are required to determine whether early migrants take longer to establish territories than late migrants.

The increased energy requirements of females for egg production alone could explain their later arrival. If the benefits were sufficient, however, females could arrive before the start of egg production (as is the case for female Spotted Sandpipers; Oring and Lank 1982). Thus, other factors must be important in reducing the benefits of arriving early.

Age effects.—Hypotheses similar to those for sexual differences in arrival dates can be formulated to explain differential migration among age classes of a particular sex. As with the sexual differences, however, our data for male American Redstarts indicate that although SY birds have shorter wings than older birds, the difference is not sufficient to explain their later arrival. Furthermore, there is no available evidence to indicate that the age classes differ in their wintering grounds. The most likely explanation for their late arrival is that SY males do not benefit as much from early arrival as ASY males. This could be because young males are unable to compete with older males regardless of when they arrive, as Nolan (1978) found for Prairie Warblers.

Rohwer et al. (1980) felt that differential age migration might occur only in American Redstarts, because their SY male plumage resembles that of females rather than of ASY males. However, SY males tend to arrive later than ASY males in Black-throated Blue and Prairie warblers (Hubbard 1965, Nolan 1978), and there is evidence from this study for similar patterns in other species.

The observed patterns of differential migration are most consistent with the hypothesis that old males arrive relatively early because of intrasexual competition for territories, while females and young males arrive later when food supplies are better and weather conditions less harsh. Other factors such as size and wintering distributions, although not sufficient by themselves to explain differential migration, also may be important in influencing migration dates. Further data are required to confirm the generality of these patterns, and to test some of the predictions, for example on food supply and age differences. Many of these data are already available from bird observatories and other areas where systematic bird-banding is practiced.

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